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Daily dynamics of contest behaviour in the territorial butterfly *Chrysozephyrus smaragdinus* (Bremer) (Lepidoptera, Lycaenidae)

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Abstract Males of the lycaenid butterfly *Chrysozephyrus smaragdinus* (Bremer) compete for mating territories via non-contact aerial interactions. Field observations revealed that contest duration decreased with increasing time of day. Further analysis showed that air temperature accounted for a significant amount of variability in the contest duration. Air temperature had a negative effect on contest duration, which suggests the influence of heat stress on contest behaviour of the butterfly. However, even when air temperature was taken into account, time of day had a highly significant negative effect on contest duration. A possible underlying mechanism is that males negotiate territorial status at the start of daily territorial activity, resulting in prolonged interactions at this time.

Key words Aggressiveness, territory, thermal biology, war of attrition.

Introduction

Males of many butterfly species hold mating territories over which they compete via non-contact aerial interactions (reviewed by Kemp and Wiklund, 2001), except for a few cases in which male-male contests involve direct physical conflict (Chaves *et al.*, 2006). This aerial interaction is regarded as a war of attrition, where both contestants continue to display and the one that retreats earlier is the loser (Maynard Smith, 1982). In physical battles, larger body size or developed weaponry are often determinants of the contest outcome (reviewed by Kelly, 2008). This parameter is known as resource holding power (RHP: Parker, 1974). By contrast, the determinants of RHP in wars of attrition are obscure and it is often unclear whether RHP asymmetry affects contest outcome. To date the characteristics correlated with RHP are largely unknown in butterflies (Kemp, 2002; Kemp *et al.*, 2006*a*; Takeuchi, 2006*a*) although some studies showed a relation between larger body size and contest success (Martínez-Lendech *et al.*, 2007; Peixoto and Benson, 2008). One of the key parameters in understanding wars of attrition is the duration of contests, which is considered to represent a loser's persistence (aggressiveness) because contests of this type terminate when either competitor ceases to display. Studies comparing duration of contests in flying insects under various conditions have brought much progress in our knowledge of war of attrition type contests (Alcock and Bailey, 1997; Kemp, 2000; Kemp *et al.*, 2006*a*, *b*; Takeuchi, 2006*b*). However, losers' aggressiveness is not the only factor that determines contest duration. There should exist physiological constrains. For example, in the speckled wood butterfly, *Pararge aegeria*, contest duration was negatively related to ambient temperature (Stutt and Willmer, 1998). Butterflies may give up more rapidly in higher air temperatures.

Chrysozephyrus smaragdinus (Bremer) is a univoltine lycaenid butterfly. Males occupy a small open space in forest, and compete with other males for these territories. In their con-

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tests, two males fly around each other, keeping some distance between themselves, until one of them flees. Males show territorial behaviour in the daytime. They leave territorial sites in the evening and return the next morning (Takeuchi and Imafuku, 2005*a*). Fujii (1982) described that contests of *C. smaragdinus* that occur at the beginning of daily territorial activity last longer. This may mean that long interactions are required when butterflies are establishing their territories. Prolonged interactions between neighboring territory owners at the establishment of the territory have been known in various vertebrates *(e. g.* Stamps and Krishnan, 1997; Tobias, 1997; Lamanna and Eason, 2003). However, Fujii (1982) showed no data on contest duration of *C. smaragdinus*. Even if there is a daily pattern described by Fujii (1982), it may be explained by daily changes in air temperature because behaviour of ectotherms can be expected to be affected by ambient temperature.

In this study, I observed territorial contests of *C. smaragdinus* to clarify whether there is a daily pattern in their contest duration, and whether the pattern is explained by daily changes in air temperature.

Methods

I carried out field work between 15 and 20 June 2003 in Nagano City (36°39′N, 138°10′E, 400 m in altitude), Nagano Prefecture, Japan. The study area was an artificial gap (approximately 30×20 m) in a temperate deciduous forest. The adult season of *C. smaragdinus* in this area was mid June to early July (the species is univoltine). Territorial males perched on limbs in their territories located around the edges of the forest. There were several territories around the gap. When another male flew into a territory, the territorial male rushed toward him and they performed an aerial contest around the gap.

I surveyed the study area from 9: 00 to 18: 00 each day. This time range includes all daily territorial activity of *C. smaragdinus* (Takeuchi and Imafuku, 2005*a*). When a contest occurred, the duration and the time of occurrence were recorded. Individual males were not distinguished. Air temperatures were measured hourly. A mercury thermometer was hung at a height of 1.5 m in the shade.

The duration of contests was analyzed on the basis of time of day (in minutes after 10: 00) and air temperature at the time of the contest. I performed a general liner mixed model (GLMM) using the two parameters, time of day and air temperature, as independent variables and contest duration as a dependent variable. Observation dates were treated as random effects. Contest duration was negative inverse transformed before analysis because it was strongly right skewed (Fig. 1). This transformation is suitable for this kind of data (Grafen and Hails, 2002). Since I recorded air temperatures once per hour, the measurement closest to the time when the contest occurred was used in analysis. During the territorial activity period, the difference in air temperatures between two consecutive hourly measurements was relatively small (0 to 1.6°C), therefore, hourly measurements should provide sufficient information. The GLMM was built through the lme function in nlme 3.1-89 library (Pinheiro *et al.*, 2008) for R 2.8.0 (R Development Core Team, 2008).

Results

I observed 93 contests during the six days of observations. Most contests lasted for less than 30 sec, but, the longest contest lasted for 799 sec (Fig. 1). The relationship between contest duration and time of day was shown in Fig. 2. A GLMM analysis showed that contest duration decreased both with increasing time of day and increasing air temperature (time of day: β=–0.0017, $F_{1,85}$=12.5, P=0.0005; air temperature: β=–0.027, $F_{1,85}$=4.4,

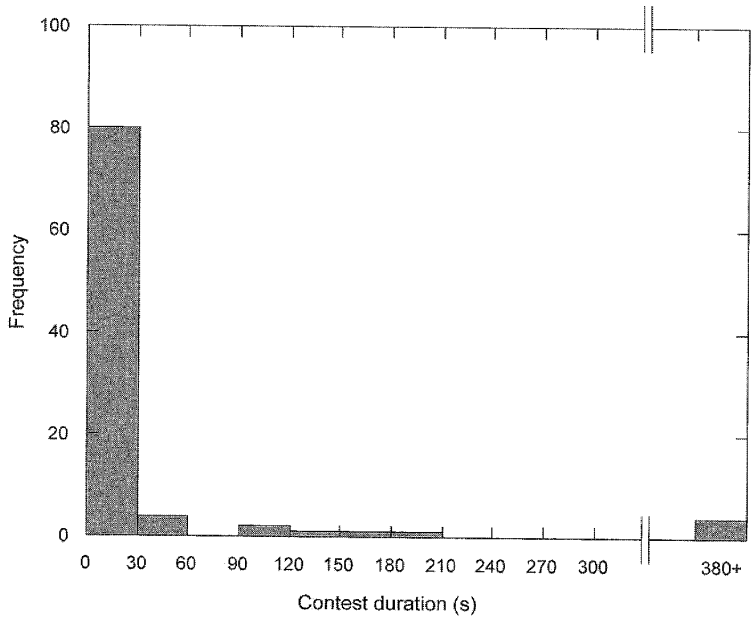

Fig. 1. Distribution of the durations of all contests. The four contests exceeding 380 sec lasted 383, 549, 656, and 799 sec.

P=0.038).

Discussion

Contest duration decreased with increasing time of day (Fig. 2). This pattern is partly explained by air temperature. As in *P. aegeria* (Stutt and Willmer, 1998), air temperature had negative effects on contest duration, which suggests the existence of heat stress on butterfly contest behaviour. In the satyrine butterfly, *Lethe diana*, males cease displaying territorial behaviour to avoid overheating in the hot season (Ide, 2002). However, even when air temperature was taken into account, time of day had a highly significant negative effect on contest duration (P=0.0005). It was evident that contests that occurred at the earlier time of day lasted longer (Fig. 2). Were males aggressive at this time? A known factor that influences the duration of contests in *C. smaragdinus* is a loser's residency period in the competed territory, because residency period and contest duration are positively related (Takeuchi, 2006*b*). During residency in a territory, individuals would acquire the motivation for competing for the territory. At the beginning of daily territorial activity, non-owner males can establish residency at territories before the owners arrive. If this is the case, non-owner males are more persistent in contests at this time than at later times, when they do not have residency because all territories are occupied by owners. Such situations were observed in *C. smaragdinus* (Takeuchi, unpubl data), and a related species, *Favonius taxila* (Takeuchi and Imafuku, 2005*b*). This is a possible cause of the daily dynamics of contest duration. Prolonged interactions often occur during territory establishment in various vertebrates perhaps because they must negotiate with neighbours for their territorial area (*e. g.* Stamps and Krishnan, 1997; Tobias, 1997; Lamanna and Eason, 2003). In butterflies, Shields (1967) described that males of *Papilio zelicon* (Lepidoptera: Papilionidae) were especially likely to engage in a battle in the morning, when territories were first established. Another possibility is that the value of territories is high early in the day, and therefore individuals are more persistent in contests. Females emerge in the morning hours in many butterfly species (*e. g.* Hirota *et al.*, 2001; Ide, 2004). In *C. smaragdinus*, it is not known when

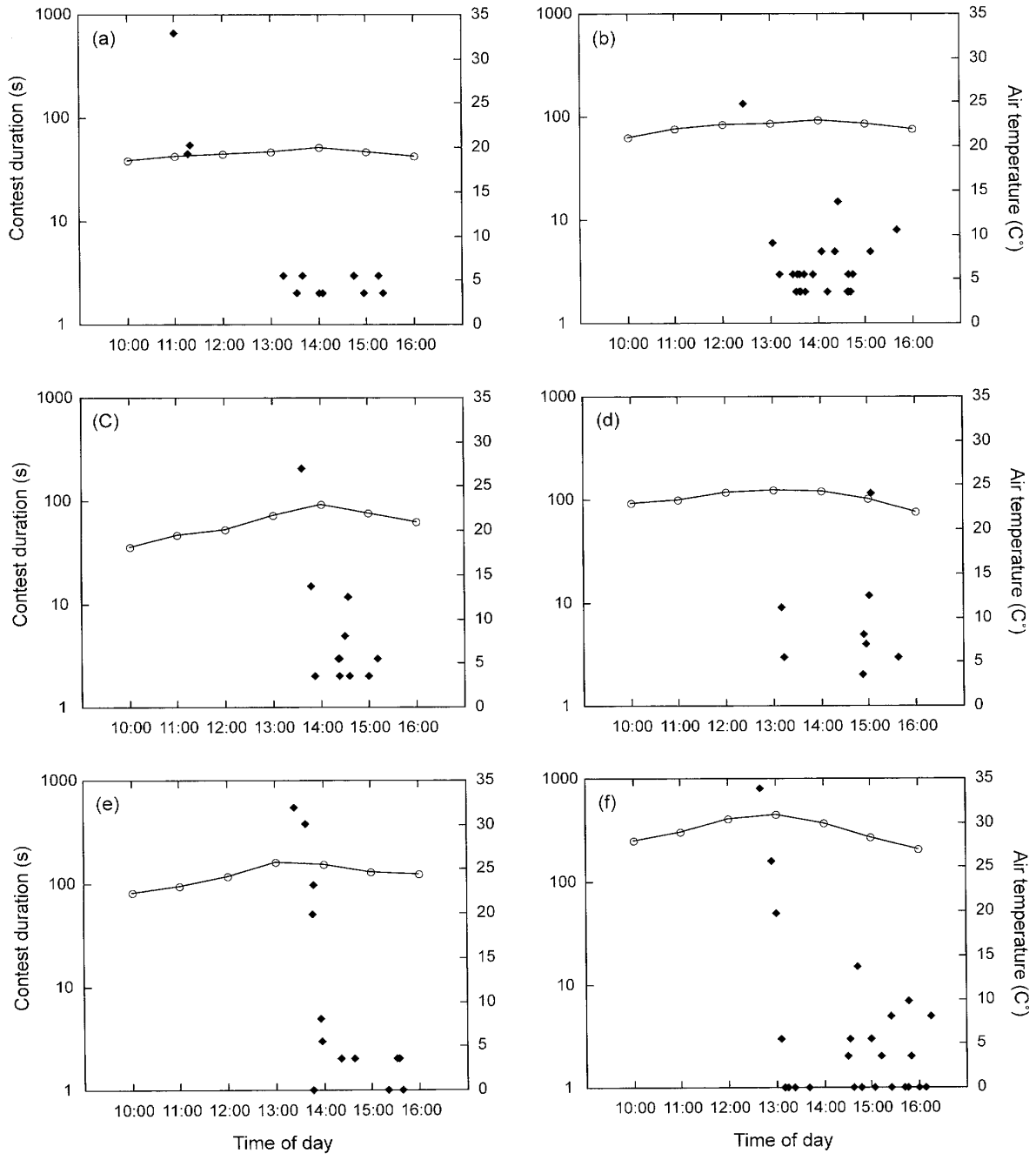

Fig. 2. The durations of contests (solid squares) and air temperature (open circles) at different times of day on June 15 (a), 16 (b), 17 (c), 18 (d), 19 (e), and 20 (f). The scale of the vertical axis for contest duration is logarithmic.

females emerge, and as is often the case with territorial butterflies (*e. g.* Cordero, 2000; Kemp, 2000), females of *C. smaragdinus* were rarely observed visiting male mating territories (Takeuchi and Imafuku, 2005*a*). At present, it is not possible to estimate the value of territories with regard to the visiting rate of females. There are other factors that influence contest duration in territorial butterflies. Contests lasted longer when male density was low in the gray hairstreak, *Strymon melinus* (Alcock and O'Neill, 1986) and in the copper, *Lycaena hippothoe* (Fischer and Fiedler, 2001). Generally, male density of *C. smaragdinus* in their territory sites was low at the beginning of daily territorial activity, subsequently in-

creased, and again decreased at the end of the daily territorial activity (Takeuchi and Imafuku, 2005*a*). If male density had a negative effect on contest duration also in *C. smaragdinus*, contests that occurred at the end of daytime should last longer. The present data did not exhibit such a tendency, leading to the conclusion that male density did not cause the daily pattern in contest duration.

At this stage, it is not possible to clearly evaluate the reasons why territorial contests of *C. smaragdinus* that occurred at the earlier time of day lasted longer. Nevertheless, this result is interesting because it implies that factors other than climatic conditions affect territorial behaviour. Further studies with individual discrimination will provide fruitful information on the territorial system of the butterfly.

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摘　　要

メスアカミドリシジミの縄張り闘争に見られる日内変動 (竹内　剛)

メスアカミドリシジミの雄は配偶縄張りを巡って, お互いに相手の周りを飛び回る闘争 (卍巴飛翔) を行う. 生息地での観察から, 日内の時刻が進むにつれて闘争時間が短くなることが明らかになった. 詳しくデータを分析したところ, 気温の変動が闘争時間の変動を部分的に説明することが分かった. 即ち, 気温が低いときの方が闘争時間は長くなる. チョウの縄張り行動に対して熱はストレスになっているのだろう. しかし, 気温の効果が考慮された上でも, 闘争の起こった時刻が早いほど, 闘争時間は長くなった. 一日の縄張り活動が始まるときには, 雄同士はお互いの縄張りを調停するために, 長い闘争が行われている可能性が考えられる.

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